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The Effect of Environment on Heritability of Yield in Spring Wheat

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THE EFFECT OF ENVIRONMENT ON HERITABILITY OF YIELD IN SPRING WHEAT

BY

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IN SPRING WHEAT

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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JJB

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INTRODUCTION

The basic objective in wheat breeding is yield improvement or stabilization. The factors upon which yield depends vary from one location to another. Water stress in Alberta, Canada, in the virtual absence of rust, is limiting on yield. In the eastern Dakotas, rust development is a prime factor affecting yield.

Frankel (11) stated that the yield of grain in wheat can be resolved into number of ears per plant, number of grains per ear and weight of grain. He indicated that these could be subject to further resolution, such as number of grains per ear into number of spikelets and number of grains per spikelet.

Many of the characters of interest to the plant breeder, and yield characters in particular, are determined both by the genotype of the plant and the environment in which it is grown. Genotype and environment interact so that such characters in segregating populations exhibit a continuous range of variability. The main theoretical problems in breeding for yield are the resolution of the variation into environmental and hereditable components and the discovery of the nature, organization and action of the hereditable component.

The primary objective of this study was to determine the effect of an environment, where supplemental moisture could be supplied and rust development was seldom serious, upon the heritability of yield in early generations of spring wheat crosses.

LITERATURE REVIEW

Hybridization among spring wheat varieties is seldom troublesome. The objectives having been set forth, one should then determine how best to accomplish them. This involves the breeding method to be followed which is most apt to provide the desired results.

Two breeding methods, or adaptations, of studying segregating populations following crossing of parent material have commonly been used to improve self-pollinated crops. Allard (2), Hayes et al. (21), Love (24) and others have outlined the essential features of the two methods which are:

1. Pedigree method

This consists of selecting parents possessing the desired characters, making the crosses, and growing the material in spaced plant rows so that plants as individuals may be studied. Records are kept, enabling one to trace individual plants from generation to generation.

Enough F_1 plants should be grown to produce the desired amount of seed for F_2. Selfs of the parent varieties should be discarded. Several thousand individually spaced plants should be grown in F_2. The F_2 selections should be grown in F_3 progeny rows. Selection commonly continues until at least the F_6 generation. When the rows are homozygous the seed is bulked and grown in yield trials. Lines not homozygous by the F_6 are generally discarded unless very promising.

2. Bulk method

The material obtained from crossing the desired parent lines is bulked in the F_2 generation and carried in bulk until the F_6. Head selection takes place in F_6 when a high proportion of the plants are homozygous for most observable characters. As an aid in selection the bulk plots can be subjected to disease epidemics or other special conditions.

The bulk method permits carrying a greater potential number of lines during the segregating generations than the pedigree method. The disadvantage is that without selection a higher proportion of the population will be undesirable. More plants would have to be selected for testing in the F_6 generation than in the pedigree method.

Sometimes a great deal can be learned about the genetics of the material during the segregating generations when the pedigree method is used. This is impossible with the bulk method.

Both systems must be evaluated in terms of the facts of genetic segregation and fluctuating environment. Also to be considered are time available, space requirements, effort that can be involved and urgency of the need for new releases.

When either of the systems are considered it must be remembered that

a. the environment is operative upon both systems

b. genetic segregation affects mainly the pedigree system

c. the loss of non-competitive, though desirable types, is most likely in bulk populations. However, some material is discarded in early generations of the pedigree system also which may have developed desirable qualities in later generations.

Because present methods of breeding are costly, laborious and lengthy it would be advantageous if selection in early generations were effective for determining higher yielding lines. Yield tests to predict the value of bulk and segregating populations have been investigated by numerous investigators. The choice of procedure in breeding is not so much in question as are solutions to the problems encountered in trying to efficiently make selections in either the bulk or pedigree method.

Favorable results supporting selection among hybrids in the F_2 generation are reported by several investigators.

Immer (22), Harrington (18) and Harlan et al. (17) have presented favorable evidence for predicting later-generation performance from early bulk-yield trials. Harrington found that bulk F_2, supplemented by bulk F_3, generation yield results accurately evaluated six wheat crosses when selected lines were tested in the F_6, F_7 and F_8 generations.

Working with barley crosses, Immer (22) suggested that the average of bulk F_2 and F_3 generation crosses would be valuable for detecting the better crosses of a group. Harlan et al. (17) carrying 379 bulked barley crosses as unselected populations for seven generations found that a preselection yield classification of the crosses agreed with the relative yield of selections made in the F_8 generations. They concluded that the low yielding crosses, constituted by the poorer types, could just as well have been discarded before selection.

Other workers have presented rather conclusive evidence that early generation bulk yield tests are not reliable standards for predicting later generation performances. Among these workers are Weiss et al. (35), Kalton (23), Atkins and Murphy (3), Fowler and Heyne (10), Suneson (32) and Grafius et al. (15).

Some of the reasons suggested for the unfavorable results were:

a. Elimination of some or many genotypes during the bulk mixture period.

Suneson (32) presented results of work carried on for 12 to 29 generations with barley that produced higher yields than those derived from conventional and more costly methods in use. He assembled and studied seed stocks of varied origins, combined them by hybridization, and bulked the F_1's. Natural selection was then permitted to sort out the best types by growing the bulks over many generations of natural cropping environments. The bulks were propagated far beyond the normal generations required for practical homozygosity. Extreme progress was shown by this method for increasing yield and adaptation. In the F_3 through F_7 generations the poorest lines occupied a very high percentage of the bulk populations. As the generations progressed single plant selections were made at the F_{20} and F_{24} generations. In replicated yield trials of 7 and 4 years, two lines of the F_{20} selections and three lines of the F_{24} selections outyielded the parent material by 37 and 56%, respectively.

Suneson and Weibe (31) studied the survival of barley and wheat varieties in mixtures. They stated that from the work of Harlan and Martini (16), who studied 11 barley varieties at locations from Oregon to New York, a direct application to bulk populations was apparent.

People using the method commonly assumed that the forces of natural selection which favor the perpetuation of plants that are best suited to survive the hybrid mixture will likewise sort out the types that will yield the best when grown alone. This assumption is probably true when the undesired types are eliminated by cold, disease or other adverse factors, but in the absence of such factors valuable materials are likely to be lost as a result of competition.

Suneson and Weibe used two widely adapted high yielding barley and wheat varieties and the results showed that when grown in mixtures with low yielding varieties they were poor competitors. They concluded that the behavior of certain varieties in mixtures suggests a decided limitation upon the success of the bulked population method of breeding when populations are carried into advanced generations.

b. Lack of correlation between yields of F_2 spaced plants and solid-row F_3 plants.

Immer (22) could not satisfactorily measure or test the yields of spaced F_2 plants in six crosses of barley. In space-planted rows the variety Minsturdi ranked second in yield while in drilled rows it ranked fifth of the six varieties in the test.

Spaced plantings of soybeans have been studied by several workers. Weiss et al. (35) and Kalton (23) found seed yields of spaced F_2 plants were of little value in the prediction of yields of F_3 and F_4 progeny. Weber (34), studying the effect of spacing, found that final differences between plant spacings within crosses were small and inconsequential. Even though initial selections were made within the same maturity class, phenotypic selection in drilled plantings resulted in slightly later maturity than selection in wider plant spacings. No differences among spacings within crosses for height and lodging were revealed.

c. Effect of dominance in the F_2, especially.

Comstock and Robinson (8) presented a model for the representation of yield. The phenotypic expression of yield (P) depends upon the genotype (Y), the environment (E) and their interaction (Y•E)

$$P = Y + E + Y \cdot E$$

In the study of yield differences involving different phenotypes or individuals, phenotypic variance is $\sigma p^2 = \sigma y^2 + \sigma e^2 + \sigma y \cdot e^2$ where p = phenotype, y = genetic effect and e = environment.

The components of total genetic variance, σy^2, were broken down into:

1. Additive genetic variance, σg^2, which is the sum of the average differences associated with the two homozygotes for each of the gene pairs that condition characteristics under selection.

2. Variance due to dominance deviations from the additive scheme, σd^2, which is the sum of the differences between the heterozygote and the average of the two homozygotes for each of the gene pairs that condition the same characteristic.

3. Variance due to epistatic deviations from the additive scheme, σv^2. Epistasis refers to types of interactions among genes or alleles not inherited in alternative, or non-allelic genes.

In segregating generations where there is appreciable heterozygosis, dominance may be extremely important in reducing heritability because the parent lines are highly selected and the additive effects have been largely eliminated (29). If dominance is a major factor as suggested by Grafius et al. (15), we may consider: $\sigma p^2 = \sigma y^2 + \sigma e^2 + \sigma y \cdot e^2$ where $\sigma y^2 = \sigma g^2 + \sigma d^2 + \sigma v^2$. In small grains, the fact of natural self-pollination makes the essential elements of gene-action in a variety additive and epistatic. Heterozygosis cannot be maintained indefinitely.

d. The role of genotype-environment interaction.

If all genotypes behaved consistently in all environments the interaction would be zero. As this is virtually unknown, the variability reflected by the interaction of genotype and environment must be accounted for and properly identified to avoid confusion in determining heritability estimates based upon additive genetic variance.

The interaction of genotype and environment has also been suggested as the cause of variability in other studies. Environment can be typed in two ways for our present purposes.

The first would involve rather severe deviations from the environment customary for a specified locale. This can be quite beneficial for selection of some specific characters. The selection for plants resistant to rusts must be performed where the incidence of the diseases is high or can be created. To test for winter hardiness the selection must be made where the winter climate is apt to be most severe. Harrington (19) selected for drouth resistance only in extremely dry years and carried on the crosses being studied as bulk populations in more favorable years.

Another desired environment is one sufficiently stable or recurring for reliable selection. Atkins and Murphy (3) classified ten bulk hybrid populations of oats as high or low yielding on the basis of bulk F_2 through F_6 generation tests. They found that as many high yielding F_7 segregates came from crosses classified as low yielding as from the high yielding group. Severe natural epiphtotics of crown rust occurred in two years and a cold wet spring was detrimental another year. They felt that conclusions on the relative yield potentialities of bulk-hybrid oat populations, based on their performance in one or two early segregating generations, would probably not be substantiated in generations where widely different growing conditions occur.

Taylor and Atkins (33) studying barley concluded that wide fluctuations in disease and climatic conditions tended to make bulk tests unreliable as a basis for selection. Bulk tests, however, may be of considerable value for prediction purposes if conducted through several years comparable for plant growth and severity of major diseases.

Fuizat and Atkins (14) felt that for simply inherited characters such as height, maturity and heading, selection is comparatively easy in barley. Many agronomic characters, however, are quantitatively inherited and highly influenced by environmental conditions. Thus it is often difficult to judge if observed variability is heritable or due to varying environment.

In studying heading dates of barley, Frey (12) stated that the most important factor contributing to heritability is its degree of expressitivity. A character highly influenced by environment tends to have low heritability. In general, complexly inherited characteristics have lower heritability than those simply inherited. Yield has a low heritability in early generations.

Mahmud and Kramer (25) reported that the effect of environment was great enough to reduce heritability estimates on early generation tests of soybean values to negligible values, while those for maturity and plant height remained higher.

Adams (1), in a South Dakota study, found that the environment had an effect on the inherent expressitivity of alfalfa clones. At the Cottonwood substation the environment was such that newly planted clones of creeping alfalfa would creep while the other types would not, whereas, at Brookings, the environment was not favorable for creeping by either type of alfalfa.

Sakai (27) studied the effects of environment on crops of rice and barley in competition. He found that a poor quality, low yielding but highly competitive variety of red-rice would out compete a good quality upland rice in any of several different planting combinations. When 12 barley varieties were grown in several ways certain ones would produce better than others, while the others were actually being depressed. The competitive ability of the F_1 barley hybrids Sakai used was generally found to be inferior to that of their parents in spite of their vigorous growth in pure stands.

Fowler and Heyne (10) felt that as long as the environment varies so greatly from season to season, even within the same location, the presently used techniques for measurement of yield will give variable results. They stated that only under rigid control of the environment will the inherent yield potential be measured accurately for any specific set of conditions.

The review of literature to this point suggests that to study the objectives set forth the pedigree system should be used. It also appears that selection studies might be more useful in early generations if at least some of the environmental variation could be reduced and perhaps thereby decrease the genotype-environment interaction to some degree.

The choice of breeding systems having been selected, it was necessary to determine how the estimates of heritability could be most satisfactorily determined.

Falconer (9) devoted nearly a chapter to the aspects of heritability. A resume of the material is presented.

Heritability expresses the proportion of the total variance that is attributable to the average effect of genes, and this in turn determines the degree of resemblance between relatives. A most important function of heritability in the genetic study of metric characters is its predictive role of expressing the reliability of the phenotypic value as a guide to breeding value. Only the phenotypic values of individuals can be measured but it is the breeding value that determines their influence on the next generation. When the plant breeder chooses individuals to be parents according to their phenotypic value, any success in changing the characteristics of the population can be predicted only from a knowledge of the degree of correspondence between phenotypic values and breeding values. The amount of correspondence is measured by the heritability.

Heritability (h^2) is defined as the ratio of additive genetic variance to phenotypic variance: $h^2 = \sigma a^2 / \sigma p^2$. An equivalent definition of heritability is the regression of breeding value on phenotypic value: $h^2 = b_{ap}$.

By regarding the heritability as the regression of breeding value on phenotypic value it becomes apparent that the best estimate of an individual's breeding value is the product of its phenotypic value and heritability, phenotypic and breeding values both being calculated as deviations from the population mean. In other words, heritability expresses the reliability of the phenotypic value as a guide to the breeding value. It is for this reason that heritability is found in nearly every formula connected with breeding methods, its magnitude often determining decisions about procedure.

Heritability is not only a property of a character but also of the population and environment to which the individuals are subjected. Since the heritability value depends upon the magnitude of all the components of variance, a change in any one of them will affect it. Gene frequencies influence all the genetic components and may differ from one population to another, depending upon the past history of the population. Small populations maintained long enough for an appreciable amount of fixation to take place are expected to show lower heritabilities than large populations. Conditions of culture or management affect the environmental variance: more uniform conditions generally increase heritability, more variable conditions reduce it. One must never forget the fact that a heritability value stated for a given character refers to a particular population under particular conditions. Other values from other populations under other conditions may be the same or different depending upon whether the makeup of the population and the environmental conditions are similar or not.

Each variety of a naturally self-fertilizing crop is a highly inbred line and the only genetic variation within a variety arises from mutation, natural crossing, mechanical mixing, or volunteering plants. Genetic improvement is made by choosing the best of the existing lines or by selection after crossing different varieties. Crossing produces genetic variation upon which selection can operate. Following the cross, the F_1 and subsequent generations are allowed to self-fertilize naturally. As the inbreeding proceeds a new population composed of differing lines develops. The genetic properties of a population derived from a cross of two highly inbred lines, such as two varieties of a self-fertilizing plant, are unique in that all segregating genes have a frequency of 0.5 in the population as a whole when selection pressures are absent.

The different relatives available determine the way in which heritability can be readily and efficiently estimated. Not only do the relatives available affect the method of determining heritability but sampling error and environmental sources of covariance also influence the decision. Environmental sources of covariance are generally more important than the statistical precision of the estimate, because the bias which may be introduced cannot be overcome by statistical procedure.

Three types of measurements are most general in use for estimating heritability, depending upon the relatives available; regression of offspring and one parent ($b = 1/2h^2$), regression of offspring and mid-parent ($b = h^2$) and correlation of half-sibs ($t = 1/4h^2$). A fourth type of heritability estimate, using the correlation of full sibs ($t > 1/2h^2$) is less desirable because components due to common environment and dominance are included causing an overestimation of heritability. When it is necessary to use full sibs the correlation obtained merely sets an upper limit to heritability.

Environment has the least influence on the half-sib correlation and the regression of the offspring on the father. Because of maternal effects, regression of offspring on the mother is likely to give too high an estimate of heritability.

Regarding precision of the estimate, the lower the sampling variance the greater the precision. For a given total number of individuals measured, the regression of mid-parental values generally yields a more precise estimate of heritability because it has considerably less sampling variance.

Nei (26), studying rice and barley, indicated that heritability estimates based upon correlation are more reliable than regression, especially if a genotype-environment interaction is present and too large to be neglected. Nei stated that even though correlation can eliminate a certain kind of genotype-environment interaction, heritability is generally overestimated.

Atkins and Murphy (3) found that correlations between successive generations for yield of bulk hybrid populations were consistently low. Bushel weight was highly correlated in successive generations and valid conclusions may be drawn from bushel weights obtained in early generations. The correlation between the F_2 - F_3 generation for yield was 0.305 while for bushel weight it was a highly significant 0.554. Correlations for yield and test weight were 0.116 and 0.673 for F_2 - F_4 generations and -0.013 and 0.416 for F_2 - F_5 generations.

Frey (12) found that the date of heading could be effectively selected for in the F_2 generation of seven barley crosses. The heritability of heading date between the F_2 and F_3 generations ranged from 47 to 92% with a mean of 76. He felt that a character highly influenced by environment would tend to have low heritability. In another study Frey (13) used F_2 and F_3 derived lines of barley. The derived line term refers to a barley strain derived from either one F_2 or one F_3 plant irrespective of the generation in which it was tested. Using the regression of the F_5 on the F_4 of F_2 derived lines the percent heritability for yield was 39, while the percentages for test weight and heading date were 96 and 93 for one cross and 53 and 85 for another cross, respectively.

Grafius et al. (15) determined heritability percentages in a bulk yield trial with barley and the percentage achieved was a low 0.046 using F_2 and F_3 plants.

MATERIALS AND METHODS

The location of the study was the U. S. Newell Irrigation and Dry Land Field Station, Newell, South Dakota. Supplemental moisture was available and could be supplied by either gravity or sprinkler irrigations. The climate is characteristic of semiarid locations where April through September rainfall averages a little over twelve inches a year, humidity is generally quite low during the daylight hours and the incidence of plant diseases is low, especially of the rusts. The last year that stem rust was especially destructive was in 1953. If it appeared that rust would develop in heavy amounts an experimental material was available to dust on the plants every week to ten days for suppression of rust development. The years the study was conducted were the driest three consecutive years of record at the Newell station since 1908. Only in 1911 had one crop season been drier.

Four varieties of hard red spring wheat were used as parents for crosses made in the greenhouse during the winter of 1958-1959. The parent varieties were recommended by V. A. Dirks, wheat breeder at that time. Two were classified as having high yield potential and two as having low yield potential.

Haynes Bluestem (CI 2874) and CI 13045, known as Bayles 10 at the South Dakota Experiment Station, were designated as high for yield potential. Reward (CI 8182) and Thatcher (CI 10003) were the parent lines of low yield potential.

Bluestem originated about 1855 and was released, after further improvement by the Minnesota Station, as Haynes Bluestem in the late 1890's. Haynes Bluestem has been described (7) as follows:

"The variety is very susceptible to stem rust. When rust is not present it yields well under humid conditions. It has long been considered an excellent milling and baking wheat."

Bayles 10 was not a commercially available variety. It had been included in regional spring wheat trials in 1952 and 1953. In 1952, grown at 10 stations, its yield averaged 135% of Thatcher. Grown at 19 cooperating locations in 1953 its yield averaged 120% of Thatcher. No records of further testing were found. Apparently it lacked desirable characteristics for commercial production and was dropped from yield trials.

Reward was developed in 1911 at Ottawa, Canada. It has been described (7) as follows:

"Reward was registered in 1928 because of its advantages of early maturity, some degree of rust resistance, high test-weight and good quality for breadmaking. In 1935 it was recognized as having the highest protein content of commercial varieties of hard spring wheat grown in the United States."

Thatcher was selected at Minnesota in 1925 and distributed for commercial growing in 1934. Thatcher was described (5) as follows:

"Thatcher is resistant to stem rust (except 15B) but is susceptible to leaf rust. It has short straw and is resistant to lodging and shattering. It has strong gluten and is very satisfactory for breadmaking. Its test weight is relatively low."

Diallel crosses were made using all four parents to secure a minimum of 50 seeds of each cross. The crosses are identified in Table 1.

Table 1. Identification of the spring wheat crosses.

Cross number	Material crossed	Yield potential
1	Bayles 10 x Haynes Bluestem	High x High
2	Bayles 10 x Thatcher	High x Low
3	Bayles 10 x Reward	High x Low
4	Haynes Bluestem x Reward	High x Low
5	Haynes Bluestem x Thatcher	High x Low
6	Reward x Thatcher	Low x Low

The F_1 plants were grown in the field at Newell during the summer of 1959. The seeds were placed in the ground in groups of 16 each in a 4 x 4 plot, the kernels spaced one foot apart. Three groups of 16 kernels of each cross were seeded for a total of 48 kernels. The location of the three groups of 16 seeds each was randomized in the field in an area 20 by 45 feet. Thatcher was seeded for border material two feet out in all directions from the plots. Some kernels either failed to germinate or died soon after emerging. Oats was seeded in these missing plots to provide more uniform competition for moisture and nutrients among the remaining plants. When the seed was mature the F_1 plants were pulled, allowed to dry, threshed in a head thresher, and the seeds counted and weighed.

A flow diagram is presented in Figure 1 to pictorially represent steps followed during the study.

A total of 1,050 kernels of each cross was used for the F_2 seeding in 1960. Three groups of 350 kernels each were placed six inches apart in the row, the rows spaced one foot apart. Natural rainfall was limited in the spring of 1960 so three inches of water were applied by sprinkler irrigation in early May. Oats was again used in the missing

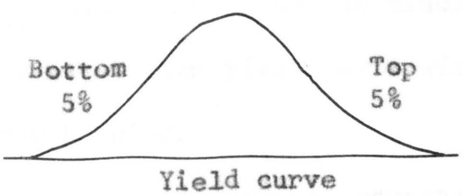
Step		Legend
Step 1	Haynes B. ↔ Bayles 10 Reward ↔ Thatcher	Reciprocal crosses made in greenhouse, 1958-59. Minimum, 50 kernels of each.
Step 2	x x x x x x x x X 3 x x x x x x x x	Three groups of sixteen F_1 kernels each cross seeded in 4 x 4 plots. The kernels were spaced 1 foot apart in each direction. Total kernels of each cross plant, 48. 1959.
Step 3	x x x x x - 350 x x x x x - 350 x x x x x - 350 cross total 1050	Three groups of 350 kernels of each cross space-seeded in rows one foot apart, six inches apart in the row. Total F_2 seeded, 1050 kernels of each plus 350 kernels of each parent line. 1960.
Step 4		The top and bottom 5% of each group of each cross for all crosses was determined after all F_2 material was threshed, cleaned and weighed. Winter 1960-61.
Step 5	*********** 50/row upper 5% *********** middle 5% lower 5% ***********	The top and bottom 5% of yield curve plus 5% from the middle of each yield curve were seeded, 50 seeds to five feet of row, the rows 2 feet apart. 1961.

Figure 1. Flow diagram of material used in the study of spring wheat crosses at the Newell Field Station, Newell, South Dakota 1959-1961.

plots to provide uniform competition. The nursery was gravity irrigated in late June to provide additional soil moisture. Rain and cooler weather in July delayed ripening until late in the month. Harvesting of the spring wheat began on August 1 and continued as the plants ripened. The plants were pulled and 20 to 25 plants of each cross were bagged together.

The plants were separated and threshed separately in a head thresher, cleaned and weighed. The material was weighed to the hundredth of a gram on a torsion balance. As each plant yield was weighed, it was identified for future use. When weighing was completed on all groups of each cross, the top and bottom 5% of each yield curve was determined in each group.

The F_3 planting was composed of the top 5% of each group of each cross, an equal number from the middle portion of the yield curve and the bottom 5% of each yield curve with a minimum of fifty available kernels per F_2 plot.

Each F_3 yield plot was composed of 50 kernels seeded in five feet of row, the rows placed two feet apart. The entire area was sprinkler irrigated following seeding to promote rapid and uniform germination.

The plots were cultivated twice, followed shortly thereafter with an irrigation by sprinklers. The plant rows were harvested as they matured from July 12 through 16, 1961. When dry, the material was threshed in a head thresher, cleaned and weighed.

To maintain adequate fertility conditions, approximately 50 pounds per acre of available nitrogen as ammonium nitrate were broadcast on the plot area each year just prior to disking. The F_1 and F_3 plantings were on the same piece of land.

DISCUSSION OF RESULTS

Chi-Square tests for homogeniety of variance

Before proceeding to analyze the variance of the F_3 yields, tests for the homogeniety of variance were run on the data. It was found that the variances were heterogeneous in the third replication (Table 2). Next an attempt was made to determine homogeniety of the variance by

Table 2. Chi-square tests of homogeniety on F_3 yield values, using either the original or transformed (log x + 1) data.

Type of comparison	DF	Value	F at .05
Original data			
Replication I	17	18.3547	N.S.
Replication II	17	7.6557	N.S.
Replication III	17	29.1136	*
Transformed data (log x + 1)			
Replication I	17	34.4637	**
Replication II	17	7.3573	N.S.
Replication III	17	15.2892	N.S.
Combining all replications	17	5.3379	N.S.
Lower 5% - Rep. I	5	2.2528	N.S.
Middle 5% - Rep. I	5	7.4834	N.S.
Upper 5% - Rep. I	5	17.3756	*
Original data			
Replication III deleting two smallest values	17	26.8774	N.S.

using the transformation of (log x + 1) as indicated by Bartlett (4). Homogeniety was achieved in all sets of data except the high 5% group of replication I. Attention was again turned to analyzing the data in their original form. Inasmuch as there were unequal subclass numbers and the error was heterogeneous, entries with the smallest yield values were omitted as suggested by Steel and Torrie (30) and the test rerun. Two small yield values in treatments with the largest numbers of values were omitted and homogeniety was achieved. The homogeneous data were used in securing all values in the following section. The yield values for the analysis of the F_3 data are recorded in the Appendix.

Analysis of variance of F_3 yield values

Foresight was not exercised to such a degree that equal numbers of entries were planted for all subclasses. Had the numbers been equal initially it is not certain that natural conditions and genetic segregation might not have eliminated some entries leaving disproportionate subclass numbers in the end. The total number of F_3 entries in each subclass was based upon the total number of surviving plants in each grouping of F_2 crosses. The total number varied in the F_2 and the subsequent 5% levels planted in the F_3 were unequal. Table 3 presents the total number that were available for analysis at the conclusion of the F_3 yield test.

Analyses of variance of unequal subclass numbers have been divided into three main classes. Steel and Torrie (30) list the following categories:

1. Data may be in a one-way classification with unequal numbers in each treatment. This is a simple factor experiment.
2. Data may be in a two-way classification with proportional subclass numbers.
3. Subclass numbers classified in more than one direction may be disproportionate.

Category three is the class into which the obtained data fall.

Table 3. The number of individual yield values obtained at the conclusion of the F_3 yield test.

Level	Cross	Replication I	II	III
Lower 5%	1	11	10	12
	2	13	10	10
	3	13	10	12
	4	11	12	10
	5	12	9	11
	6	11	6	9
Middle 5%	1	11	10	11
	2	13	10	10
	3	13	12	11
	4	11	12	11
	5	12	9	11
	6	11	6	9
Upper 5%	1	11	10	12
	2	13	10	10
	3	13	11	12
	4	10	12	11
	5	12	9	11
	6	11	6	9

It was initially planned that inferences could be drawn from two classes of data; that obtained by grouping the results of the F_2 generation into high and low levels and, from the results of the various crosses. Had the study been repeated, over time and/or space, the same classes of data would have been studied and the effects would not be studied at random but on a fixed criterion.

The material assigned to each replication was on a random basis as the F_1 material counted out for planting in the F_2 generation was composited prior to planting. The effects of replications are considered to be random.

Thus, with levels and crosses regarded as fixed and replications regarded as random a mixed model occurred. The model for analyzing the data was:

$$X_{lcrk} = \mu + A_l + B_c + C_r + AB_{lc} + AC_{lr} + BC_{cr} + E_{lcrk}$$

where X_{lcrk} is the observation of the k^{th} plant in the r^{th} replication, the c^{th} cross and l^{th} level.

μ - is the average effect common to all individuals in the experiment.

A_l - refers to the effect common to all individuals in the l^{th} level causing them to deviate from the population average.

B_c - refers to the effect common to all individuals in the c^{th} cross causing them to deviate from the population average.

C_r - refers to the effect common to all individuals in the r^{th} replication causing them to deviate from the population average.

AB_{lc} - refers to the interaction effect between level l and cross c causing an observation which receives both effects to deviate from the average of the combined effects.

AC_{lr} - refers to the interaction effect between level l and replication r causing an observation which receives both effects to deviate from the average of combined effects.

BC_{cr} - refers to the interaction effect between cross c and replication r causing an observation which receives both effects to deviate from the average of combined effects.

E_{lcrk} - is the random effect causing the different individuals to deviate from the average of the l^{th} level, c^{th} class and r^{th} replicate.

The analysis of variance was performed on an electronic computer. Dr. W. L. Tucker, Experiment Station Statistician, set up the analysis based upon a program developed by Harvey (20).

The mean square expectation values (Table 4) were determined by the methods outlined by Schultz (28). As the sampling method leads to

Table 4. The structural analysis and mean square expectations for the F_3 yield data.

Source of variation	Degrees of freedom	Mean square expectations
Total	575	
Sums of squares due to reduction	33	
A - levels	2	$\sigma_e^2 + k_6 \sigma_{lr}^2 + k_8 \sigma_l^2$
B - crosses	5	$\sigma_e^2 + k_5 \sigma_{cr}^2 + k_7 \sigma_c^2$
C - replications	2	$\sigma_e^2 + k_4 \sigma_r^2$
AB - levels x crosses	10	$\sigma_e^2 + k_3 \sigma_{lc}^2$
AC - levels x replications	4	$\sigma_e^2 + k_2 \sigma_{lr}^2$
BC - crosses x replications	10	$\sigma_e^2 + k_1 \sigma_{cr}^2$
Error	542	σ_e^2

cross classification of fixed and random effects, those interactions involved gave rise to components which were random in one direction only; they were measured over the random variate, replications.

The final outcome of the analysis of variance as presented in Table 5 did not indicate statistical significance for either levels or crosses using the data obtained. This is contrary to what might have been expected. Preliminary perusal of the table suggests that significance for both levels and crosses has been established. However, the F values for levels and crosses were not determined by using the error mean square term. These two classifications have been determined to be fixed, thus assuming the total population has been included and no component of uncertainty remains as all the population was sampled.

The tests for significance of levels can be determined by using the mean square values of levels x replications. This is because some random variation from replications is included in this term. Similarly, the test for significance of crosses is measured by the crosses x

Table 5. Analysis of variance for the 1961 F_3 yield data, in grams, using the least squares method.

Source of variation	Degrees of freedom		Sums of squares	Mean square
Total	575		889.54741	
Sums of squares due to reduction	33		109.69299	3.32403
Levels		2	2.06161	1.03070
Crosses		5	5.56358	1.11271
Replications		2	51.37644	25.68822**
Levels x crosses		10	.84939	.08493
Levels x replications		4	1.97024	.49256
Crosses x replications		10	8.34626	.83462*
Error	542		147.62227	.27236

* Significant at .05 level.
** Significant at .01 level.

replications mean square and does not approach significance.

There are two possible factors favoring an outcome of statistical significance. Initially, the parent lines were selected as having either a high or low yield potential. It might be expected that this selection in itself would favor certain crosses over others. Secondly, following classification of the F_2 yield data, selection was exercised again in favor of the high and low yielding lines.

Because significance was not obtained for either levels or crosses it is somewhat difficult to develop any positive statements. Before proceeding to develop further comments it was decided to determine whether the parent lines reacted as initially stated in regard to yielding ability.

The parent material was grown each year. In 1960, the material was neither replicated nor randomized with the F_2. The parent lines were randomly placed in each replication five times in the 1961 F_3

planting. An analysis of variance of the 1961 planting is presented in Table 6.

Table 6. Analysis of variance of parent material grown in conjunction with the F_3 yield test, 1961.

Source of variation	Degrees of freedom	Sums of squares	Mean square
Total	59	37098.44	
Varieties	3	2249.78	749.92
Replications	2	11183.88	5591.94**
Varieties x replications	6	1074.52	179.08
Error	48	14508.19	302.25

** Significant at .01 level.

The average yields of the parent lines grown in 1960 and 1961 did not respond as initially suggested. In the 1960 trial of spaced plants, the two parent lines chosen for high yielding ability were lowest in yield. In the 1961 trial when the material was planted in rows, one of the parents chosen as low, Thatcher, was again at the top for yield but Reward dropped to become the poorest yielding variety. It becomes quite apparent that the parent material should have been selected on the basis of several years yield trials in the environment in which the study was located, not upon results in the more humid, lower elevations of the eastern Dakotas and Minnesota.

The following comments are observations developed from Tables 7 and 8. In Table 7 the effect of selection for plants in the lower and upper levels indicates that it was effective to some degree. The deviation from the mean for low yielding plants, -.0756, was of greater magnitude than the increase in yield for plants in the upper yield curve.

Table 7. The over-all mean and level, cross and replication deviations from the mean in the F_3 tests.

Category	Over-all mean grams	Deviation from mean grams
Levels		
Lower 5%	1.0632	-.0756
Middle 5%	1.0632	0.0034
Upper 5%	1.0632	0.0722
Crosses		
1 - H x H	1.0632	-.1302
2 - H x L	1.0632	0.1038
3 - H x L	1.0632	-.1091
4 - H x L	1.0632	0.1273
5 - H x L	1.0632	0.0101
6 - L x L	1.0632	-.0019
Replications		
I	1.0632	0.3206
II	1.0632	0.0712
III	1.0632	-.3919

The negative departure, -.1302, from the mean for Cross 1, supposedly a cross of two high yielding parents, is somewhat surprising. However, considering the yields achieved when the parent material was grown at the same time the F_2 and F_3 plantings were grown, it may be that below average yield should have been expected.

The significant effect of replications is rather obvious upon examination of the array of replication deviations. Perhaps these wide deviations or variations masked the effect of the other classifications and negated possible favorable results.

The least squares estimates presented in Table 8 compare in degree to the values obtained for the original data in Table 2 when tests were made for homogeniety of variance. The smallest values were

Table 8. Least square estimates of the various replication x cross interaction components in the F_3 tests.

Replications	Crosses 1	2	3	4	5	6
I	1.2901	1.5218	1.2502	1.3840	1.5261	1.3153
II	0.9978	1.3289	1.1087	1.3038	1.1896	0.8623
III	1.2855	1.4244	1.2775	1.6578	1.2783	1.7918

obtained for data in replication II and the largest in replication III.

It becomes increasingly apparent that the differences in replications outweighed the differences derived from either levels or crosses. Explanations for this difference in replication response are not offered as management practices were the same over the entire plot.

Heritability estimates

In the review of literature it was indicated that the heritability estimates with the lowest sampling variances would be obtained by the regression of the yield values obtained from the F_3 generation upon the values obtained when the F_2 generation was grown.

Individual yield values, in grams, were obtained for each of the F_2 and F_3 progeny plantings used in this study. Linear regressions, based upon F_3 progeny yield values regressed upon their F_2 mid-parent values, were determined.

The heritability values, i.e. regression coefficients, for all six crosses at each of three designated levels are presented in Table 9. Accompanying each value is the confidence interval for beta, the population regression parameter estimated by the heritability value. The

Table 9. Linear regression coefficients and the confidence intervals for beta at t = .05 for the six crosses used based on F_3 progeny mean yields regressed on F_2 plant yield values.

	Percent of F_2 Yield Curve					
	Lower 5%		Middle 5%		Upper 5%	
Cross	b	error	b	error	b	error
1	0.2026	± 0.4183	0.1504	± 0.1650	0.0976	± 0.0286
2	0.1606	± 0.3762	0.0439	± 0.1025	-.0226	± 0.0436
3	0.4068	± 0.3334	-.1141	± 0.1003	0.0246	± 0.0444
4	1.2792	± 0.6600	0.0080	± 0.0620	0.0557	± 0.0359
5	0.2784	± 0.3139	0.2419	± 0.0465	0.0576	± 0.0322
6	0.3438	± 0.5726	-.5839	± 0.3885	0.0484	± 0.0452

heritability estimates were rather erratic within levels and more so between levels of the various crosses.

The data indicate that only a small amount of heritable variation for yield was obtained in the higher levels. In using the confidence intervals derived, comparisons indicate only a small percentage of variation was present, be it the high x high cross, low x low cross, or crosses between high x low parents.

Although no conclusive statements can be developed it is interesting to observe the range of variability found in the lower level. If any responses were noted it was the inequality of the responses to selection in opposite directions. It might be expected that any response achieved would be symmetrical for both ends of the curve. The asymmetric response obtained will be discussed though no positive statements are possible.

Initially, the F_2 plants harvested were categorized and the plants falling in the bottom and top 5% of each yield curve were determined. In striving to more closely approximate conditions under which a crop may be normally grown in the field by farmers, the F_3 progeny were seeded in rows, 50 kernels to the row. In doing this a certain portion of the F_2 progeny falling at the extreme lower end of the yield curve of each cross were by-passed to secure the lower 5% with a minimum of 50 kernels, the number chosen as necessary for seeding in each row. This initial truncation placed the portion of the curve sampled not at the extreme lower end of the curve, but anywhere from 4 to 32 plants in from the lower end of the curve. By so doing, the plants which may have been homozygous or nearly so were not used and the material seeded was in a more highly heterozygous condition, giving a measure of higher variability, i.e. heritability value.

Falconer (9) indicates that asymmetry of response has been found in many two-way selection experiments, but its cause is not yet known. He notes several possible causes which are selection differential, "genetic asymmetry," selection for heterozygotes, inbreeding depression and maternal effects. Of those listed perhaps the second and fourth could further affect the results found in this study in addition to the previous discussion.

Within the initial population there are two sorts of asymmetry in the genetic properties that could give rise to asymmetry of response. These concern the dominance and the gene frequencies of the loci concerned with the character. It is possible that the dominant alleles at each locus are mostly those that affect the character in one direction, instead of being distributed nearly equally between those that increase and those that decrease. Falconer (9) referred to this situation as directional dominance. If the initial gene frequencies were at about 0.5, the response would be expected to be greater in the direction in which the alleles tend to be recessive. Therefore, in general, characters that show inbreeding depression could be expected to respond more rapidly to downward selection than to upward selection. He also suggests that inbreeding depression upon a character may cause the mean to decline during inbreeding. This reduces the rate of response in the upward direction and increases it in the downward direction, again giving rise to asymmetry.

The previous discussion no doubt raises questions as to how well the suggested possibilities apply to wheat, a naturally self-fertilizing plant. For many years the expression has been made that the variety is "running-out." This was generally answered by expressing the belief that better varieties had been developed or new diseases reduced the yields. Although these were true, recent work begun on hybrid wheat suggests that inbreeding can and does take place. Unpublished data from the South Dakota station and reports by Briggle (6) indicate that hybrid vigor is present in wheat. In some instances yields of 25% or more than the yield of the parents have been obtained in the F_1. The possibility of growing the F_2 seed is considered questionable as, in the case of hybrid corn, it may lose its yield advantages because the variability combined for high yield in the F_1 is reduced in subsequent generations.

The values presented in Table 10 are the result of pooling data within levels, ignoring the various crosses. Considering first pooling

Table 10. Linear regression coefficients and the confidence intervals for beta at t = .05 for the various 5% levels of all crosses.

Level	Heritability estimate and error
Lower 5% - all crosses	0.2693 ± 0.1566
Middle 5% - all crosses	0.0068 ± 0.0278
Upper 5% - all crosses	0.0236 ± 0.0001
Lower 5% - high x low crosses	0.2972 ± 0.1819
Middle 5% - high x low crosses	0.0575 ± 0.0402
Upper 5% - high x low crosses	0.0342 ± 0.0196

of all entries at the various levels, it is obvious that the heritability estimate (0.2693) for the lower 5% of the yield curve contains much more variability than either of the other two levels. The result found for the middle portion representatives is as one might expect because this portion has come from the part of the curve which is most heterozygous. Apparently little progress has been made at the upper end of the yield curve if the value shown (0.0236) is an estimate of any value.

The crosses were made initially from parents classed as being either high or low in yielding ability. The variability that may be derived when high x high or low x low crosses are made could possibly be quite restricted. An analysis excluding these possible deterants to improving heritability values was next undertaken. The results, shown in the lower portion of Table 10, are from pooling across the four crosses classified as high x low. Some improvement was obtained in the size of the values for each level. This may indicate that some restrictions were present in the two crosses excluded when the heritabilities for the high x low crosses were calculated.

The result of pooling across all levels within each cross are presented in Table 11. At first glance it appears that nothing was accomplished. Actually it substantiates the fact that selection at either end of the yield curve was quite critical. The figures were derived by pooling the data from all three levels within a cross, accounting for but 15% of the original population curve. The original

Table 11. Linear regression coefficients and the confidence intervals for beta at t = .05 for the six crosses used based on F_3 progeny yields regressed on F_2 plant yield values.

Cross	Heritability estimate and error
1	0.0170 ± 0.0072
2	0.0072 ± 0.0094
3	0.0097 ± 0.0086
4	0.0112 ± 0.0087
5	0.0083 ± 0.0093
6	0.0104 ± 0.0137
highs x lows (2-5)	0.0090 ± 0.0045

population was considered to have zero variability. By pooling all data for a cross the effects of selecting for levels are stabilized and the values deviate only slightly from the zero values assumed for the original cross populations.

The high x low cross values were pooled across levels in all four crosses and a result similar to those obtained by pooling across individual crosses was obtained. Pooling reduced the error to half the heritability estimate.

SUMMARY

The yielding ability of six crosses of hard red spring wheat was studied in space-planted F_2 trials and drilled F_3 trials at the Newell Field Station during 1960 and 1961. The drilled F_3 trials represented the upper, lower and middle 5% of the F_2 yield curve of each replication of each cross. The location was favored because of low incidence of diseases and availability of irrigation water, possibly permitting greater expression of yield potential in the plants.

Heritability estimates derived from the F_3 progeny mean yields regressed on F_2 plant yield values were erratic in response and indicated that a nonheritable fraction of genetic variance probably comprised the major portion of genetic variance at that phase.

Chi-square tests for homogeneity of variance indicated that the material, taken all together or as individual replications, was a uniform test of the same population. The value for one replication was just within the limits required for homogeneity.

Statistical significance was obtained for only replications and replications x crosses interaction. Other analyses of the F_3 yield data provided nonsignificant results.

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APPENDIX A

Table A-1. The gram mean values used in the analysis of variance of the F_3 yield data.

Portion of yield curve								
Upper 5%			Middle 5%			Lower 5%		
Replication			Replication			Replication		
I	II	III	I	II	III	I	II	III
Cross 1 - Haynes Bluestem x Bayles 10								
2.130	0.620	0.830	0.920	0.240	0.160	1.240	1.090	0.330
0.980	1.340	1.750	1.260	1.030	0.500	1.010	0.900	0.390
1.390	1.200	0.090	1.570	0.460	0.160	1.350	0.970	0.590
0.470	0.600	0.700	1.140	1.350	0.660	1.120	0.200	0.490
1.390	1.300	0.005	1.920	1.320	1.320	0.660	0.430	0.410
1.800	1.160	0.450	1.200	0.780	0.590	0.680	1.250	0.650
1.490	1.490	0.730	0.790	0.850	0.490	0.890	2.500	0.350
1.880	0.220	1.550	1.270	0.370	0.420	0.140	1.190	1.210
2.090	1.200	0.380	1.870	2.530	0.470	1.800	0.690	0.120
1.890	1.540	0.030	1.070	0.380	0.090	1.190	0.830	0.240
1.080		0.240	1.810		0.010	1.190		0.220
Cross 2 - Bayles 10 x Thatcher								
1.330	1.180	1.160	1.180	1.060	0.001	1.260	1.450	1.490
1.260	1.090	0.150	1.120	1.240	0.860	1.490	2.600	0.260
2.010	2.150	0.590	1.490	0.810	1.360	1.630	0.980	0.360
1.610	1.800	0.020	0.940	0.240	0.450	2.050	0.610	1.170
2.020	1.150	0.110	1.510	1.450	0.100	1.320	1.460	0.670
1.370	1.810	0.750	1.980	1.420	0.670	0.930	0.970	0.030
1.620	0.290	1.130	1.550	2.720	0.570	1.800	0.720	0.110
1.120	1.360	1.100	2.130	1.490	1.080	1.310	1.110	0.180
1.700	1.310	0.680	1.270	1.060	1.040	1.800	1.740	1.220
1.840	1.680	1.650	2.170	0.600	0.320	0.440	2.420	0.030
1.350			1.390			1.580		
2.220			1.820			1.430		
2.110			1.520			0.810		

Table A-1 Continued.

Portion of yield curve								
Upper 5%			Middle 5%			Lower 5%		
Replication			Replication			Replication		
I	II	III	I	II	III	I	II	III
			Cross 3 - Bayles 10 x Reward					
1.860	0.590	0.330	1.600	1.730	0.230	1.520	1.580	0.430
1.370	0.590	1.010	0.710	2.360	0.190	2.090	0.430	0.970
1.080	1.920	1.430	1.510	2.050	0.650	0.890	0.370	0.070
2.200	0.380	1.110	1.290	2.280	0.160	1.810	0.210	0.490
2.120	1.670	0.010	1.630	1.650	0.040	1.030	0.320	0.270
1.100	0.930	0.070	1.360	1.070	0.070	1.060	1.210	1.420
1.140	1.110	0.350	1.440	1.490	0.300	0.540	0.570	0.920
1.430	1.280	0.290	1.190	1.350	0.910	0.510	1.420	0.530
0.460	0.750	0.090	1.410	0.700	0.390	0.890	0.670	0.007
1.030	2.030	0.030	1.720	0.920	0.650	2.030	0.660	0.110
0.650	1.330	0.970	0.930	0.070	0.640	1.370		0.790
1.690		1.470	1.040	1.280		0.550		0.006
1.420			0.300			0.910		
			Cross 4 - Haynes Bluestem x Reward					
1.850	2.180	1.030	0.990	2.350	1.090	1.030	1.230	0.960
1.590	2.150	1.260	1.690	1.780	0.780	1.700	1.420	1.880
1.880	1.140	0.620	1.300	1.000	1.360	1.970	2.020	1.900
1.770	1.080	0.530	1.230	0.450	1.580	0.540	1.850	2.100
1.890	2.060	1.670	1.050	1.190	0.810	1.900	1.300	0.390
1.480	1.120	0.050	1.940	1.350	0.990	0.700	0.470	1.100
0.770	2.260	1.030	1.200	1.340	0.020	0.910	0.210	0.810
2.060	1.410	0.370	1.940	1.830	0.060	1.350	1.000	0.003
1.210	1.300	0.030	1.560	1.410	0.040	0.840	0.960	0.110
1.170	1.370	1.890	1.870	0.810	0.970	0.330	1.460	
	1.340	0.110	0.740	1.270	1.560	1.850	0.840	
	0.220			0.680			1.210	